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THE CONSPECIFICITY OF HETEROSIPHONIA ASYMMETRIA
AND H. DENSIVUSCULA AND THEIR
LIFE HISTORIES IN CULTURE

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INTRODUCTION

The marine red algal genus *Heterosiphonia* (Ceramiales, Dasyaceae) includes about 40 species which are widely distributed in temperate, tropical and cold waters. The genus is characterized as having polysiphonous and corticated main axes which branch in a sympodial manner. The lateral branches are alternate, distichous and either monosiphonous or polysiphonous. Spermatangia and tetrasporangia are borne in specialized conical reproductive structures called stichidia (Kylin, 1956).

On the Pacific coast of North America five species are known. *Heterosiphonia densiuscula* and *H. laxa* were described from Friday Harbor, Washington by Kylin (1925). Both species are known only from northern Washington and southern British Columbia (Scagel, 1957). *Heterosiphonia asymmetria*, described by Hollenberg (1945), has a range extending from Santa Catalina Island to the Monterey Peninsula in California (Hollenberg and Abbott, 1966). Gardner (1927) described *H. erecta* which ranges from southern California to Baja, California (Dawson, 1963). *Heterosiphonia wurdemannii* Børgesen is broadly distributed in tropical waters and is present in the Gulf of California (Dawson, 1963).

Heterosiphonia erecta and *H. wurdemannii* are described as having four pericentral cells, *H. asymmetria* as having five, and *H. laxa* and *H. densiuscula* as having six to nine. The first two species appear to be morphologically distinct taxa, but *H. asymmetria*, *H. densiuscula* and possibly *H. laxa* appear very closely related, if not identical, for reasons which will be brought out in the observations and discussion section of this paper. Because of the apparent taxonomic problems involving these three species, I considered it necessary to re-investigate various aspects of their morphology and life histories.

MATERIALS AND METHODS

For the culture of *H. densiuscula*, specimens were dredged from about 15 m depth at Partridge Bank, west of Whidbey I., Washington, on July 6, 1965. This clone has been maintained for over four year in unialgal culture with Provasoli's enriched seawater medium (Provasoli, 1966) in 10 C, 16 hr daily photoperiod and 20–40 ft-c cool white fluorescent lighting. The clone of *H. asymmetria* was isolated from material collected in the drift at the south end of Carmel Beach, Monterey Peninsula, California, April 19, 1967. It has been cultured for more than two years in 15 C, 15–150 ft-c cool white lighting and 16 hr daily photoperiod with Provasoli's medium.

All seawater for these culture studies was obtained from the Bodega Marine Laboratory, Bodega Bay, California. It was aged at least 30 days in the dark at 20–22 C before use. The salinity was adjusted to 30–31‰ by adding glass distilled water. The seawater was then steam sterilized for 30 minutes and stored until use. The enrichment medium was added to the sterile seawater just prior to use.

All cultures were maintained in either Pyrex (No. 3250) 100 x 80 deep storage dishes with 150–200 ml of the medium or in Pyrex 90 x 50 mm crystallizing dishes with 100 ml of the medium.

Tetraspores were allowed to attach to coverslips which were transferred to fresh medium every 14–30 days.

OBSERVATIONS AND DISCUSSION

Culture studies. *Heterosiphonia densiuscula* grows well in culture without significant deviation from the morphology observed in field-collected specimens. The initially tetrasporophytes produced tetraspores which gave rise to tetrasporangia-bearing plants after 3 months at about 30 ft-c illumination. The plants in culture are 3.0 to 5.0 cm long when reproductive, in contrast to plants from nature which often reach 10 to 15 cm in length when reproductive. Neither carpogonia nor spermatangia were observed on any of more than 500 plants from four successive generations. The tetrasporangia are normal in morphology and release 4 spores. Each fertile segment of the stichidium bears 4 to 6 sporangia in a whorl (fig. 2). Spore germination is similar to that described for most of the Ceramiales. The spore first divides into two unequal cells. The smaller cell is the initial of the basal system. It forms either an elongate multicellular rhizoid or a multicellular lobed at-

FIGS. 1–5. 1–4, *Heterosiphonia densiuscula*; 5, *H. asymmetria*; 1, 2, same scale; 1, apex of cultured plant, sympedial, alternate, distichous branching of main polysiphonous branch is evident; 2, cultured tetrasporophyte with pedicellate stichidium borne on polysiphonous basal portion of lateral branch; 3, squashed preparation of type specimen showing branch bearing five pericentral cells enclosing axial cell (ac); 4, young germling in monosiphonous stage, new apical meristem developing from intercalary cell and multicellular lobed attachment organs are evident; 5, habit photograph of typical specimen collected from same location at same date as cultured specimen.

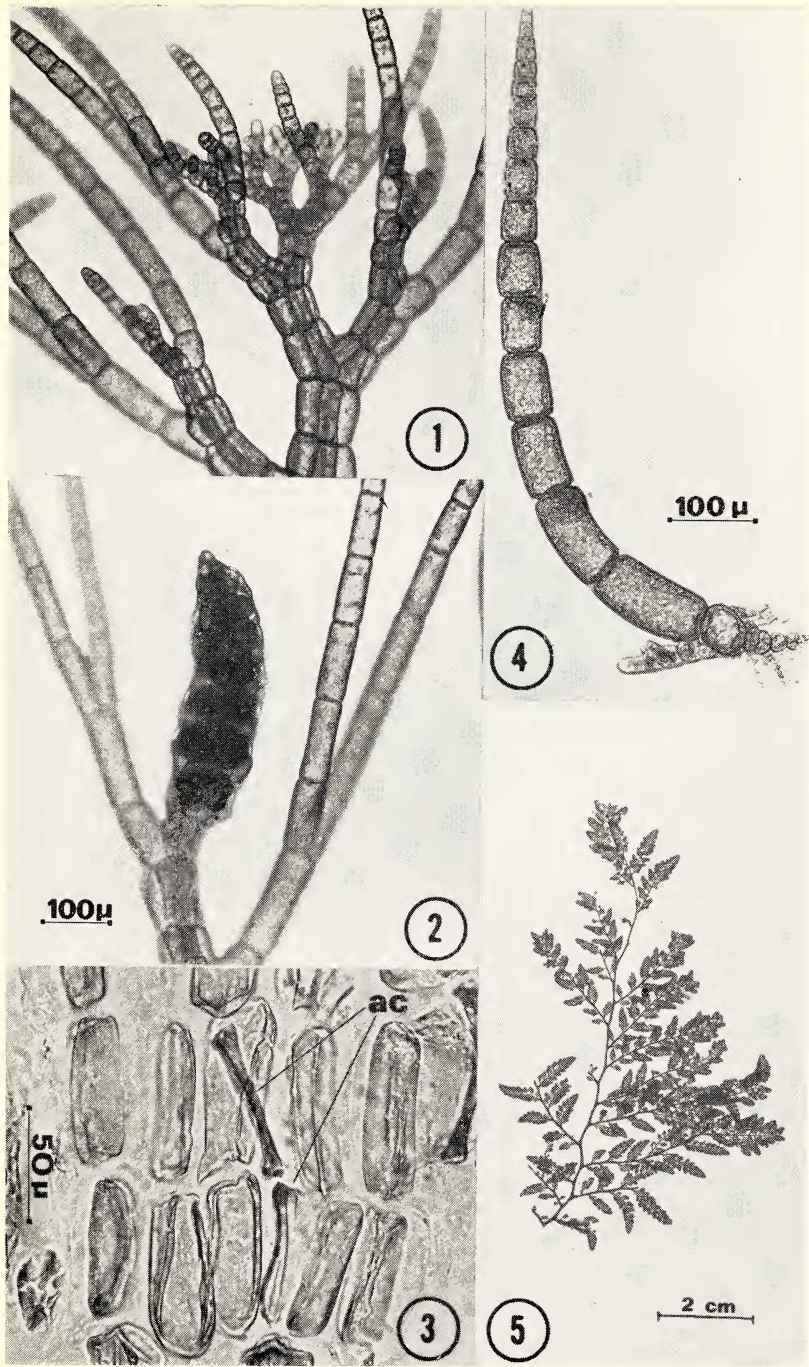




FIG. 6. *Heterosiphonia densiuscula*, habit photograph of typical specimen dredged from Hein Bank, south of San Juan I., Washington.

tachment disk (fig. 4). The larger of the two cells derived from spore division is the precursor of the erect system. When the primary erect monosiphonous filament becomes about 1 mm in length, the apical meristem begins to branch sympodially. Additional meristems may be established from intercalary cells by an oblique lateral division which produces a new initial (fig. 4). The meristems give rise to the polysiphonous sympodially branched axes of the developing plant (fig. 1).

Heterosiphonia asymmetria cultures also were started from a field-collected tetrasporophyte and the tetraspores also gave rise to tetrasporangia-bearing plants for two successive generations. The cultured plants were much smaller than plants from nature, rarely exceeding

1.0 cm in length. The third generation is morphologically aberrant and does not grow well but it is being maintained for further study. It grows primarily by proliferation of the uniseriately filamentous basal system from which occasionally arise erect polysiphonous branches that bear tetrasporangia.

Heterosiphonia densiuscula cannot tolerate light intensities above 50 ft.-c. Above 75 ft.-c the germlings bleach and die within a week. On the other hand, *H. asymmetria* grows and reproduces in intensities from 15 to 150 ft.-c.

Morphological studies on field-collected specimens. The types of *H. densiuscula* and *H. laxa* were re-examined and found to have only 5 pericentral cells per segment instead of 6-9 as recorded in the original description (Kylin, 1925). Kylin's own figure (fig. 44, p. 68) shows only three pericentral cells on one side which is indicative of five or, at the most, six. Re-examination of *H. asymmetria* type specimen reveals 5 pericentral cells per segment as indicated in the original description (Hollenberg, 1945). The pericentral cells of all three species are characteristically arranged so that three are evident in face view on one side of the branch and two are seen on the opposite side when the branch is turned over.

Although all three species are similar, an insufficient number of *H. laxa* specimens are available for a thorough re-examination of its morphology. A comparison of the major morphological characteristics of *H. densiuscula* and *H. asymmetria* (table 1) indicates that clear similarities exist.

The reproductive patterns of life histories of these two species also appear similar. A survey of *H. densiuscula* from several herbaria shows that of approximately 110 specimens, 95% bear tetrasporangia and the remaining 5% are sterile. The original description likewise refers only to tetrasporangiate plants. Recently, however, male and female gametophytes were collected by Michael Wynne from Puget Sound in Washington. Mature cystocarps were present on the female plants indicating that both sexes possess functional sexual structures. The presence of gametophytes, even though they are extremely scarce, suggests that this species exhibits two types of life histories in the same locality. It is possible that two distinct genetic races have developed, one exhibiting the typical sexual red algal life history and the other exhibiting a non-sexual type. Gametophytes are not yet available for a culture study.

A survey of *H. asymmetria* herbarium specimens from the Monterey Peninsula reveals that 44 of 45 plants examined are tetrasporophytes. The remaining plant is sterile. To the best of my knowledge gametophytes have been collected only twice. The type specimen is a male collected February 12, 1938 from Corona Del Mar, Orange Co., California. Two cystocarpic female specimens were collected by E. Yale Dawson from White's Cove on Santa Catalina Island, California, October 31, 1948. It is apparent in this case that on the Monterey Peninsula a type

TABLE 1. MORPHOLOGICAL COMPARISON OF *HETEROSIPHONIA ASYMMETRIA* AND *H. DENSIUSCULA*.

	<i>H. asymmetria</i>	<i>H. densiuscula</i>
Main branches		
sympodial, distichous and alternate	+	+
Main branches (1st & 2nd orders)		
lacking pubescence of monosiphonous branchlets	+	+
Number of segments between branch	2-3	2
Ratio of dimensions of segments	0.5 to 1.5 x as long as broad	0.5 to 1.5 x as long as broad
Number of pericentral cells	5	5
Arrangement of pericentral cells (in side view)	transverse to slightly asymmetric	transverse to slightly asymmetric
Arrangement of pericentral cells (in cross section)	3 + 2	3 + 2
Cortication by longitudinal filaments derived from pericentral cells	+	+
Stichida on monosiphonous & poysiphonous branchlets	+	+
Stichidia pedicellate or sessile	+	+
Pedicels monosiphonous or polysiphonous	+	+
	3-5	4-6
Number of sporangia/fertile segment in stichidium	up to 800 μ	up to 800 μ
Maximum diameter of main axis	up to 15 cm	up to 15 cm
Total height of plants	intertidal & subtidal	subtidal
Habitat		

of life history similar to that observed for *H. densiuscula* occurs. Male and female plants are reported only from the southern limits of its range in California which suggests that only certain populations may exhibit a life history characteristic for the higher Florideophyceae. However, tetrasporophytes are not known to occur in the same locality.

The tetrasporangia from field-collected specimens of both species appear normal morphologically and form tetrads of spores but evidently are mitotic, in most instances, rather than meiotic, because in the cultured clones tetrasporophytes develop repeatedly.

Although the non-sexual type of life history is not common among the higher Florideophyceae, there is good evidence that some species are represented only by the tetrasporophytes in nature. Svedelius (1937) demonstrated that tetrasporangia of *Lomentaria rosea* are apomeiotic. Sparling (1961) noted that *Halosaccion glandiforme* (Gmelin) Ruprecht and *Rhodymenia palmata* f. *mollis* Setchell and Gardner never or very rarely have been found to bear spermatia, carpogonia or cystocarps. She maintained tetraspore germlings of both species in culture for about 2 years, but was not able to observe any reproduction. This suggests, at least, that heteromorphic gametophytes and tetrasporophytes do not occur in these species and that mitotic tetraspores are the only means of reproduction.

On the basis of their morphological similarities and the evident similarities in their life histories *H. asymmetria* Hollenberg should be considered a synonym of *H. densiuscula* Kylin. *Heterosiphonia laxa* and *H. densiuscula* also appear closely related. In addition, as *H. laxa* is separated from *H. densiuscula* only by the comparative sparsity of branching in the former, it cannot be concluded at this time that it is conspecific. Insufficient material is available for morphological comparison and no living plants are available for culture. Moreover, all three phases of *H. laxa* frequently occur in nature, indicating that it may have a typical sexual life history.

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SUMMARY

Similarities in the morphology and life histories of *H. asymmetria* and *H. densiuscula* indicate that they are conspecific. The two clones studied in cultures formed successive generations of tetrasporophytes. This correlates well with information on the field collected plants, 95% or more of which are also tetrasporophytes.

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